

Eudolium crosseanum (Monterosato, 1869), Biacores sta. 161, the Azores, 37°40'N, 25°51'W, 590 m, young specimen, height 26.1 mm (MNHN). Figures 11, 78, 79.

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Oocorys sulcata (Fischer, 1883), off S Portugal, Noratlante sta. B12, 36°22'N, 08°43'W, 2873 m (MNHN). Figures 15, 16, 24, 50, 150–152.

Oocorys abyssorum (Verrill & S. Smith, 1884), SE Atlantic, Vema sta. CP02, 11°00'N, 45°15'W, 5073 m (MNHN). Figure 66.

Oocorys bartschi Rehder, 1943, Pequegnat 68 A13 sta. 22, 27°38'N, 95°22'W, 476 m (MNHN). Figure 119.

Oocorys umbilicata Quinn, 1980, Gulf of Mexico, 21°30.3'N, 96°11.7'W, 2245 m (MNHN). Figure 118.

Galeodea echinophora (Linné, 1758), Mediterranean, Golfo di Genova, Sori, 35–55 m (SMNH 476). Figures 17, 18, 22, 51.

Galeodea echinophora, Mediterranean, Corsica, off Calvi, 50–70 m (SMNH). Figure 120.

Cypraecassis testiculus (Linné, 1758), larva, Dana sta. 1286: V, 15°17'N, 61°29'W, plankton (ZMC). Figures 23, 115–117.

Semicassis granulatum (Born, 1779), Mediterranean, Golfo di Genova, Sori, 20–30 m (SMNH 475). Figures 19, 20.

Semicassis sp. aff. *granulatum* (Born, 1778), Dana sta. 1353, 33°51'N, 66°43'W, plankton (ZMC). Figures 63, 64.

Semicassis granulatum, no loc. (SMNH). Figure 65.

Semicassis saburon (Bruguère, 1792), N'Diogo sta. 5, 17°26'N, 16°39'W, 500 m (MNHN). Figure 21.

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Pisanianura grimaldii, New Caledonia, Biocal sta. DW51, 23°05'S, 167°45'E, 680–700 m (MNHN). Figures 25, 26, 55, 68.

Pisanianura grimaldii, Biocal sta. DW51, 23°05'S, 167°45'E, 680–700 m (MNHN). Figure 95.

Pisanianura grimaldii, R/V *Vauban* sta. CH22, 12°27'S, 40°10'E, 680–700 m (MNHN). Figures 94, 127.

Pisanianura grimaldii, holotype, Azores (MOM), 27.6 mm. Figure 126.

Pisanianura breviaxe, Biocal sta. CP52, 23°06'S, 167°47'E, 540–600 m (MNHN). Figures 27, 123, 153, 154.

Pisanianura breviaxe, holotype, off Kochi Pref., Japan (NSMT Mo 38611). Figure 124.

Pisanianura inflata (Brocchi, 1814), Pradalbino, prov. Bologna, Italy, Pliocene, deep-water deposits (Coll. della Bella). Figures 93, 125.

Kaiparanura spiralis (Marshall, 1918), holotype (NZGS Tm 6921), Pakaurangi Point, Kaipara Harbour, New Zealand, Altonian or more probably Ofaian age (Lower Miocene, A. Beu, pers. comm.). Figures 144, 145.

Kaiparanura spiralis, 1 mile NW of Pakaurangi Point,

Kaipara Harbour, New Zealand (NMNZ M 81338). Figures 142, 143.

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Ranella olearia, Balgim sta. CP25, 36°41.5'N, 07°19.4'W, 544 m (MNHN). Figures 87, 88.

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Sassia raulini (Cossmann & Peyrot, 1923), Chattian, Upper Oligocene of Bassin de l'Adour, coll. Lozouet (MNHN). Figure 90.

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Reproductive Systems of Neritimorph Archaeogastropods from the Eastern Pacific, with Special Reference to *Nerita funiculata* Menke, 1851

by

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Abstract. Differences in reproductive anatomy occur among the eastern Pacific neritimorph gastropod genera. These differences are based on the location of the accessory sperm sacs in the female and the nature of the copulatory organ in males. Also, there appears to be a direct relationship between the spermatophoric filament and the length of the duct to the receptaculum seminis. In addition, a sorting mechanism has been demonstrated to occur within the crystal sac of *Nerita funiculata*.

INTRODUCTION

The Neritimorpha have a nearly world-wide distribution but as a group it is mostly limited to subtropical and tropical habitats. According to RUSSELL (1941) temperature is probably the limiting factor in the distribution of species from this suborder. Much of the systematic and anatomical work has been on the neritimorphs of the eastern and western Atlantic and the Indo-Pacific (ANDREWS, 1937; BERGH, 1890; BOURNE, 1908; FRETTER, 1946, 1965, 1966; LENSSEN, 1899; STARMÜHLNER, 1969, 1976, 1983; THIELE, 1902, 1929). Studies on the eastern Pacific neritimorphs have been neglected because the United States Pacific coast lacks a tropical fauna and, until recently, access to many of the tropical west American habitats has been difficult. According to KEEN (1971) only eight species of neritimorphs belonging to five genera have been described from the tropical eastern Pacific. Most of the morphological studies on eastern Pacific prosobranchs have been on caenogastropods from the Gulf of California (HOUSTON, 1976, 1985).

It is, therefore, valuable to study the reproductive systems of these eastern Pacific species in order to compare them to the genitalia of previously studied species. Also important is close examination of the anatomy and function of the spermatophores and such female organs as the crystal sac and capsule gland. These organs were previously studied by ANDREWS (1933, 1935, 1937) in several species of western Atlantic neritids. The species examined in the

present study are *Nerita scabricosta* Lamarck, 1822, *Nerita funiculata* Menke, 1851, *Neritina latissima* Broderip, 1853, *Theodoxus luteofasciatus* Miller, 1879, and *Titiscania limacina* (Bergh, 1875). According to KEEN (1971), both *N. funiculata* and *T. luteofasciatus* occur throughout the Gulf of California and southward to Peru. *Nerita scabricosta* is also found throughout the Gulf of California but extends only as far south as Equador. *Titiscania limacina* is uncommon but has been observed from the northern Gulf of California to Panama. In contrast, *Neritina latissima* does not occur within the Gulf of California but ranges from Equador to only as far north as Acapulco, Mexico.

MATERIALS AND METHODS

Living specimens were collected from the following areas: *Nerita funiculata*, Coloradito, Baja California Norte; *Nerita scabricosta*, Puertecitos, Baja California Norte, Puerto Peñasco, Sonora, and Punta Chivato, Baja California Sur; and *Theodoxus luteofasciatus*, Bahía Concepción, Baja California Sur. Specimens of *Neritina latissima*, Isla del Coco, Costa Rica, and *Titiscania limacina*, San Carlos, Mexico, were studied using material loaned by the Los Angeles County Museum of Natural History. Descriptions of the genitalia were made after careful dissections of both preserved and living material (preserved only for *Neritina* and *Titiscania*); stained sections were examined in order to elucidate cellular details. The soft parts were relaxed in propylene phenoxytol (OWEN, 1955) and fixed in Bouin's

fluid. Sectioned material was then stained with Kornhouser's hemalum, eosin B, and Alcian blue. Ciliary currents were observed by using suspended carmine particles in seawater.

RESULTS

Nerita funiculata

The male duct (Figure 1A): In living males the testis is bright orange and shares the visceral mass with the digestive gland. From the testis a thin-walled straight gonadal vas deferens runs down the right side of the digestive gland until it reaches the posterior end of the pallial duct. Here it becomes highly convoluted and glandular. During the breeding season, which occurs from late spring through summer, the vas deferens is packed with spermatozoa and functions as a seminal vesicle. This tube enters the pallial duct ventrally about one-third of the distance along its length.

In this species the pallial duct is suspended from the right wall of the mantle cavity. In addition, in living specimens it appears as an elongate white glandular mass that is closed throughout its entire length. Histological sections reveal that it is really two separate glands, an anterior prostate and a posterior auxiliary gland. The anterior one-half of the prostate is composed of numerous acini that are lined with alternating ciliated and eosinophilic staining gland cells. Posteriorly these cells give way to basophilic staining cells. However, just before entering the auxiliary gland there are two lateral strips of mucous cells. In this region the seminal vesicle becomes the pallial duct. The lumen of the prostate bifurcates, sending one branch posteriorly while the other switches back in an anterior direction. In the auxiliary gland the cells stain bright red and are filled with many small spherical inclusions. There are no ciliated cells in this region.

The genital opening lies dorsal to and well in front of the anus. It is lined with ciliated cells alternating with mucous cells and is surrounded by a thin sheet of circular muscle fibers. In this species the penis is a dorsoventrally flattened triangular flap situated between the cephalic tentacles and attached along its posterior edge. A ciliated groove begins at the tip and runs along the right side of the organ until it disappears into a small pouch at the base. In living individuals the genital aperture can be observed lying close to the base of the penis, although there is no direct connection.

The male gametes are stored in spermatophores, which are transferred to the female during mating. These structures measure 2 to 2.5 mm in length and have a fusiform body that is blunt at one end. As shown in Figure 2, a long filament arises from the rounded end and is wrapped around the body in a spiral fashion. Cross sections show the filament to be hollow.

The female duct (Figure 3A): The female system of this species is diaulic with both nidamental and genital open-

ings lying adjacent to one another next to the anus. Between the nidamental opening and the anus there is a flap of tissue that acts as a valve that closes off the former during the release of fecal pellets. In living individuals the white ovary occupies almost the entire visceral mass during the summer mating season. From the ovary a ciliated, thin-walled oviduct winds down the right side of the visceral mass and joins the posterior region of the pallial oviduct. Just before entering the pallial region there is a small opening from the oviduct into the mantle cavity. In mature specimens the large cream-colored capsule gland extends from just beneath the mantle edge to the extreme posterior region of the mantle cavity. As in males, the pallial oviduct is suspended from the right mantle wall. The nidamental opening is lined with low columnar ciliated cells. Just posterior to this opening there is a bifurcation with one duct leading to the capsule gland and the other to the crystal sac. This sac is a thin-walled, bulbous pouch that begins on the right side of the capsule gland and swings over onto the dorsal surface. The anterolateral wall of this organ is lined with mucous cells that constitute a mucous pad. The medial wall is lined with low columnar cells from which arises a ciliated groove that runs dorsad into the proximal region of the sac. Here, this groove opens directly into the ventromedial wall that is thrown into a series of complex ciliated folds (Figure 4). The functions of these folds will be discussed later. The dorsolateral wall is smooth and non-ciliated.

The ciliated lumen of the voluminous capsule gland appears as a dorsoventral crescent with the concave side facing left. The staining characteristics of this organ are as follows:

Cell Type I—Subepithelial eosinophilic gland cells with round basal nuclei. These cells occur in clusters that open into the lumen via common ducts. Moreover, these cells constitute the ventral and lateral walls of the entire capsule gland.

Cell Type II—These cells have flat basal nuclei and a colorless cytoplasm. In addition, they are arranged as acini and lie dorsal to the lumen.

Cell Type III—Mucous cells that are sandwiched between the lumen and cell type II.

Figure 5 is a diagram of the ciliary currents within a capsule gland that was opened along the mid-dorsal line. About two-thirds of the way through the capsule gland the lumen divides into two lateral branches. In this region the right branch becomes the posterior end of the capsule gland while the left leads to the albumin gland. In the albumin gland a fourth cell type that stains turquoise with Alcian blue occurs. This gland is bilobed and is referred to as the upper and lower albumin glands. In the lumen of the lower albumin gland there is a ventral ciliated groove that bifurcates, with one branch leading to the oviduct and the other to the fertilization chamber. This sac is really

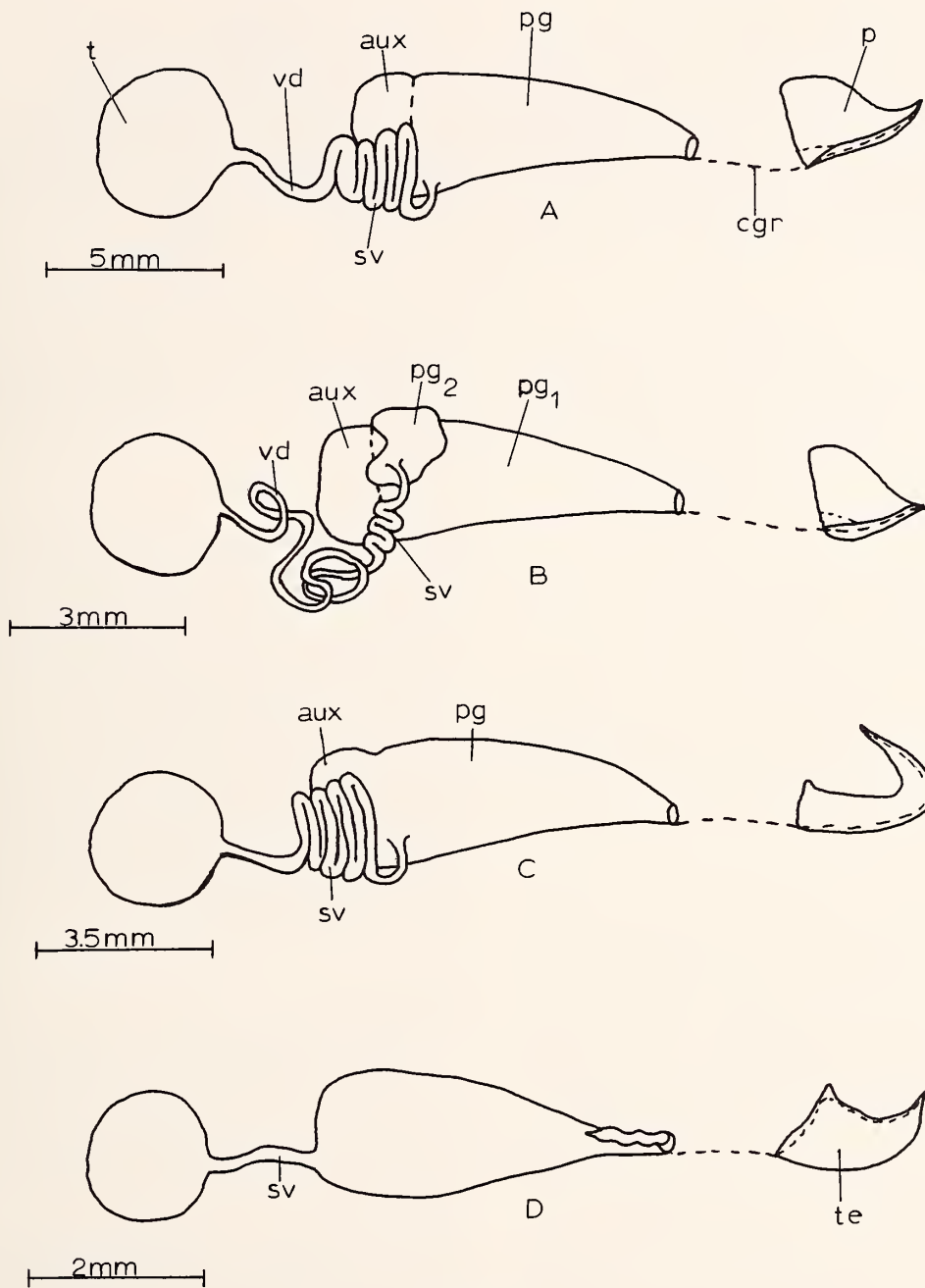


Figure 1

Diagrammatic reconstructions of the male genital ducts. A. *Nerita funiculata* and *Nerita scabricosta*. B. *Theodoxus luteofasciatus*. C. *Neritina latissima*. D. *Titiscania limacina*. aux, auxiliary gland; cgr, ciliated groove; p, penis; pg, prostate gland; sv, seminal vesicle; t, testis; te, tentacle; vd, vas deferens.

an expanded, thin-walled region of the receptaculum seminis. The walls opposite the fertilization chamber are composed of numerous acini lined with tall columnar cells. These acini empty into a ciliated trough that opens directly into the fertilization chamber and that also communicates with the duct to the spermatophore sac. In cross section

the acini appear circular and are packed with sperm oriented with their heads toward the center and their tails attached to the epithelium. In addition, the receptaculum seminis also seems to function as an ingesting gland, for pieces of spermatozoa can be observed with vacuoles of some of the acinar epithelial cells. A convoluted duct leaves

this organ and continues in an anterior direction for some distance, then abruptly switches back to enter the spermatophore sac. This elongate muscular pouch is about one-half the length of the capsule gland and is full of spermatophores in mating individuals. Near its proximal end is the opening to the long muscular sperm duct, which runs anteriorly and terminates at the genital pore.

For the following species only major differences in their anatomy will be noted.

Nerita scabricosta

The only noteworthy difference for this species is the absence of an opening to the mantle cavity from the posterior region of the oviduct (Figure 3B, see arrow). Otherwise the reproductive systems are essentially the same as for the previous species.

Theodoxus luteofasciatus

The male duct (Figure 1B): (a) A second prostate gland seems to lie between the seminal vesicle and the anterior prostate. (b) The seminal vesicle is much larger than in *Nerita* and it also differs in being proximally coiled.

The female duct (Figure 3C): (a) A separate duct joins the albumin gland with the spermatophore sac. (b) The receptaculum seminis is a small bulbous organ located at the end of a long duct that leads directly to the albumin gland.

Neritina latissima

The male duct (Figure 1C): (a) The most noteworthy difference is the morphology of the copulatory organ. The penis, instead of being a triangular flap, is cylindrical and distally tapers to a point. A ciliated groove begins just proximal to the tip and continues posteriorly along the dorsal surface to the head where it ends just behind the right cephalic tentacle. In addition, a flap of tissue can be observed covering this groove except for the extreme distal end. (b) The spermatophores are similar to those of *Nerita* except that the filaments are much shorter.

The female duct (Figure 3D): The histology for this species is similar to that of *Nerita*. However, there are some major differences in the gross anatomy. (a) The system is triaulic with the presence of a ductus enigmaticus. This duct, originally described by BOURNE (1908), branches off the sperm duct just anterior to where the duct from the receptaculum joins the spermatophoric duct. This convoluted canal can be seen as it passes forward alongside the capsule gland and then straightens out distally just before opening into the mantle cavity. (b) The spermatophore sac is spherical and is only about one-fourth the length of the capsule gland. Up to four spermatophores were observed inside this organ. (c) The duct that joins the spermatophore sac to the receptaculum seminis is straight and short. (d) There is no opening from the go-

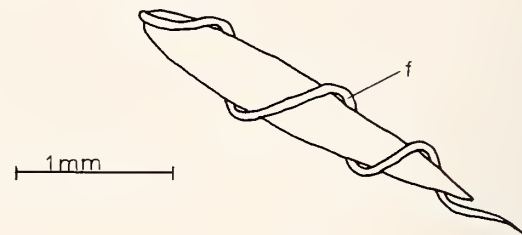


Figure 2

A spermatophore from *Nerita funiculata*. f, filament.

nadal oviduct into the mantle cavity. (e) The crystal sac, which appears to be filled primarily with sand grains, lies on the left side, dorsal to the distal region of the capsule gland.

Titiscania limacina

The male duct (Figure 1D): (a) The seminal vesicle is straight, not convoluted. (b) No accessory prostate gland was observed. (c) The genital opening is bordered by two tissue flaps that lead to a ciliated groove that passes to the right side of the head. (d) There is no separate penis. However, the right cephalic tentacle is enlarged and may function as the intromittent organ.

The female duct (Figure 3E): (a) The spermatophore sac is elongate and S-shaped. (b) The ductus enigmaticus and crystal sac are absent. (c) The receptaculum seminis is a rather large tear-drop shaped organ, which lies just posterior to the spermatophore sac. (d) The duct that joins the receptaculum seminis with the spermatophore sac is short, like that found in *Neritina*.

Reproduction in *Nerita funiculata*

The reproductive season for this species was from the last of May through September. During this time there was both extensive mating and spawning. However, during the winter months spermatozoa have been seen in the receptaculum seminis of females. Therefore, spawning individuals could possibly have mated during some prior season.

The entire mating process takes anywhere from 10 minutes to one-half hour, depending on the individual pair. Initially, the male climbs onto the right side of the shell of the female and inserts the penis into the right side of the mantle cavity. During this time the pair makes back and forth movements and simultaneously rotate to and fro through a 90 degree arc. After pausing for a period of about one minute they oscillate in the opposite direction. At this time the spermatophores are transferred to the mantle cavity of the female. When copulation is completed the male either crawls down and away or withdraws into the shell and falls off.

The egg capsule: The yellowish-white capsule is elliptical in outline and measures up to 3 mm across the long axis.

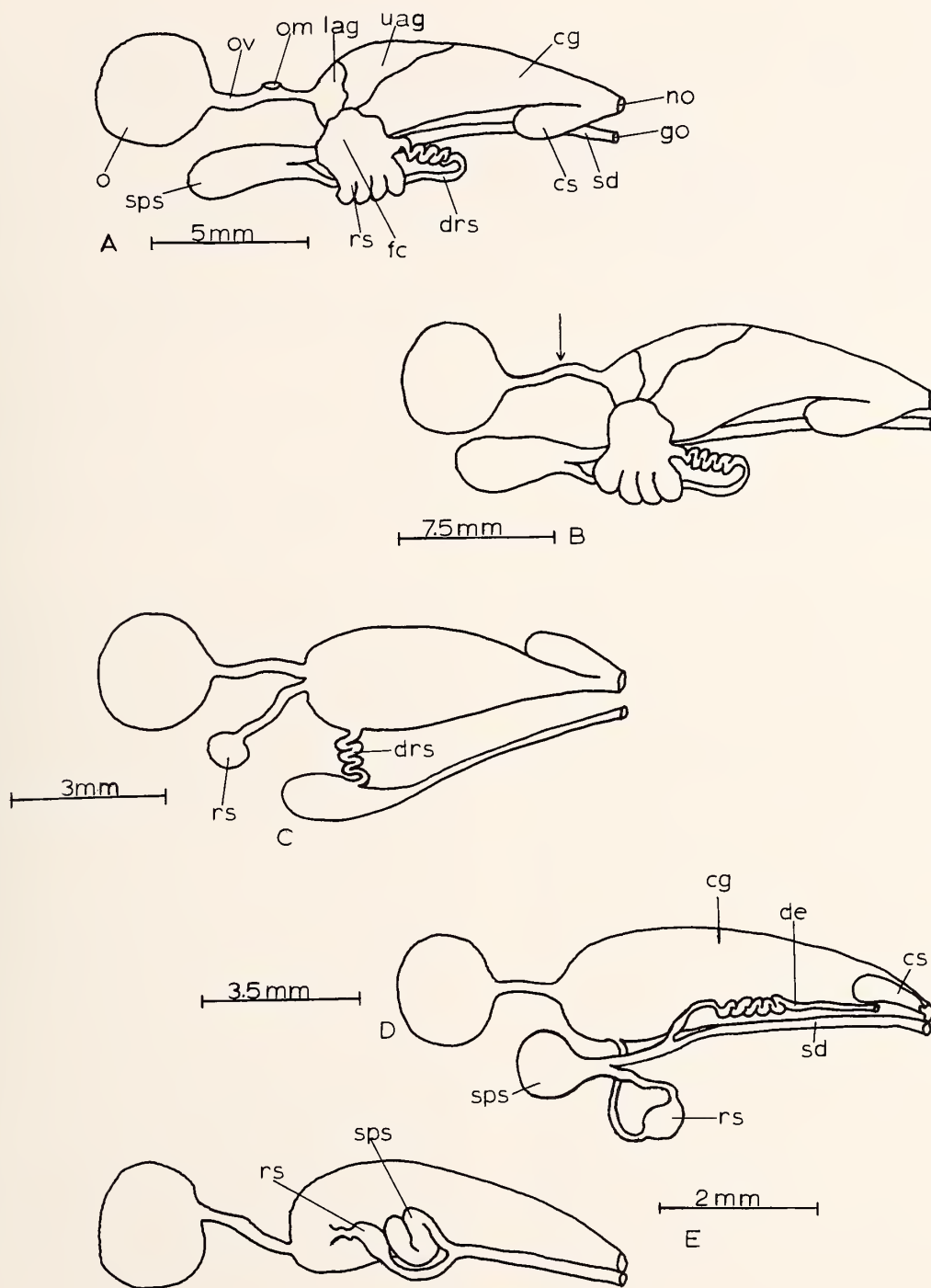


Figure 3

Diagrammatic reconstructions of the female genital ducts. A. *Nerita funiculata*. B. *Nerita scabricosta*. C. *Theodoxus luteofasciatus*. D. *Neritina latissima*. E. *Titiscania limacina*. cg, capsule gland; cs, crystal sac; drs, duct to receptaculum seminis; de, ductus enigmaticus; fc, fertilization chamber; go, genital opening; lag, lower albumin gland; no, nidamental opening; o, ovary; ov, oviduct; om, opening of oviduct into mantle cavity; rs, receptaculum seminis; sd, sperm duct; sps, spermatophore sac; uag, upper albumin gland.

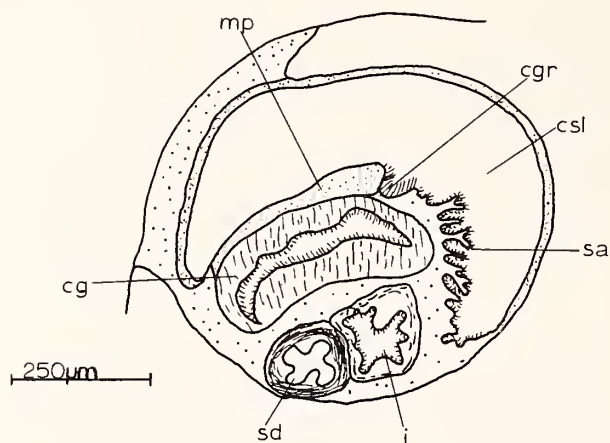


Figure 4

A cross section through the crystal sac from a female *Nerita funiculata*. cg, capsule gland; cgr, ciliated groove; csl, lumen of crystal sac; i, rectum; mp, mucous pad; sa, sorting area; sd, sperm duct.

It is composed of a lens-shaped cap sutured to a flat base that is affixed to the substratum. As shown in Figure 6, the capsule is composed of two layers. The inner homogenous layer has the same staining properties as the secretions of the capsule gland. The outer layer is a mucous coat in which are embedded spherulites. The base has the same staining qualities as the homogenous layer, except it is filled with mucous vesicles. The eggs, up to 50 in each capsule, are suspended within an albuminous secretion.

As the egg capsules are released they are sprinkled with spherulites which were stored in the crystal sac. These particles are extracted from fecal pellets as they pass from the anus. Sections of the gut reveal a heterogeneous assortment of particulates in the feces, including a variety of diatom skeletons. As this material is released from the anus into the mantle cavity, a portion is carried by cilia to the crystal sac where it is sorted and stored. On entering the sac this material becomes entangled in mucus that is secreted by the mucous pad (Figure 4). Here, this mucous string passes to the sorting area where only spherical particles are selected out while the waste is cleared back into the mantle cavity. Dissections of the crystal sac also show that most of these spherulites are of similar size. When needed, they are passed along the ciliated groove (mentioned earlier) to the outside where they become embedded in the surface of the egg capsule. Up to four layers of spherulites occur in the outer wall.

DISCUSSION

The general anatomy of reproductive systems is rather uniform among neritimorph prosobranchs. This has been substantiated in the definitive works by ANDREWS (1937) and BOURNE (1908). Moreover, in all of the species investigated in this study, the male genitalia produce spermatophores that are subsequently transferred to the female

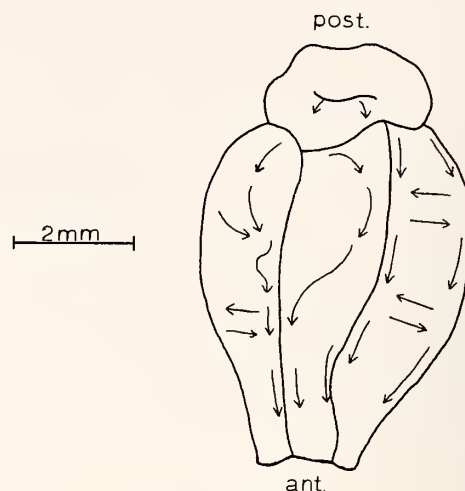


Figure 5

Ciliary currents within a capsule gland from *Nerita funiculata*. ant., anterior; post., posterior.

by a cephalic penis or some equivalent structure. In the female the spermatophores are stored in a bursa or spermatophore sac where the sperm are released and travel to the receptaculum seminis prior to fertilization. This is also the case for other neritimorphs (BERRY *et al.*, 1973; BOURNE, 1908; FRETTER, 1946, 1984; STARMÜHLNER, 1969, 1976, 1983). Although spawn was observed only for *Nerita funiculata*, its hemispherical structure is in accordance with that of other neritids, as described by ANDREWS (1935) and FRETTER (1946). Even though these similarities exist, differences are apparent in the reproductive anatomy at the generic level. Both BOURNE (1908) and ANDREWS (1937) remarked on the relationships among genera based on similarities in their anatomy. A more recent study on the anatomy of *Nerita birmanica* (Phillipi, 1844) by BERRY *et al.* (1973) has confirmed the results of the aforementioned early works. In addition, STARMÜHLNER (1969, 1976, 1983) has shown this to be true for the freshwater and brackish *Clithon*, *Neritina*, and *Septaria* from various localities throughout the Indian ocean.

In the species studied, some obvious differences between *Nerita*, *Theodoxus* and *Neritina* have not been previously mentioned. In *Nerita* the receptaculum is directly attached to the surface of the albumin gland. Internally a ciliated groove leads from the receptaculum to the fertilization chamber. In *Neritina* and *Theodoxus*, however, the receptaculum seminis is separate and is connected to the albumin gland by a well defined duct. This also appears to be the case for the Indo-Pacific neritids observed by STARMÜHLNER (1976). Furthermore, he shows that in *Neritina* and *Septaria* the bifurcation that gives rise to the duct to the receptaculum seminis occurs about halfway along the length of the sperm duct. This differs from *Neritina latissima* (and *Titiscania*) where the branching is proximal and just anterior to the spermatophore sac.